C 5

CONFERENCE OF EMPIRE METEOROLOGISTS, 1929.

AGRICULTURAL SECTION.

IMPERIAL BUREAU OF MYCOL
2 JUL 1930

Weather and Climate

In their Relation to

Insects.

LONDON:
PRINTED UNDER THE AUTHORITY OF HIS MAJESTY'S STATIONERY OFFICE
By Wyman & Sons, Ltd., Fetter Lane, London, E.C.4.

1929

CONFERENCE OF EMPIRE METEOROLOGISTS, 1929.

AGRICULTURAL SECTION.

Weather and Climate

In their Relation to

Insects.

By B. P. Uvarov,
(*Senior Assistant, Imperial Bureau of Entomology.*)

LONDON:
PRINTED UNDER THE AUTHORITY OF HIS MAJESTY'S STATIONERY OFFICE
By Wyman & Sons, Ltd., Fetter Lane, London, E.C.4.

1929

CONFERENCE OF EMPIRE METEOROLOGISTS, 1929.

AGRICULTURAL SECTION.

WEATHER AND CLIMATE IN THEIR RELATION TO INSECTS.

By B. P. UVAROV,

(*Senior Assistant, Imperial Bureau of Entomology.*)

It is not for me, an entomologist without any special knowledge of meteorology and climatology, to insist before the present Conference on the extremely complex inter-play of various meteorological elements which go to make a weather, or a climate. I am only going to attempt to show how these elements and their infinitely varying combinations influence the highly complicated organism of insects, their life and activities, many of which are of supreme importance to man, since they concern his crops, health and even life.

The numerous problems of the influence of various meteorological factors on insects have formed the subject of many special studies, and the entomological literature is full of examples of such an influence. A full survey of the literature on these problems will be given elsewhere, and in the present paper I propose only to draw the attention of the members of the Conference to some outstanding points, in particular to those in the investigation of which a close co-operation between an entomologist and a meteorologist appears absolutely essential.

Let us consider briefly the influence of each of the main meteorological factors on insects.

Temperature.—The aggregate amount of work done on the influence of temperature on insects is very considerable and the main results may be summarised very briefly as follows :—

The influence of temperature on insect activities is easily observable, since it results mainly in various more or less conspicuous movements. A general scheme for all activities of an insect as dependent on temperature is based on the conception of an optimum zone of temperature, within which all activities are most pronounced ; above this zone lies that of a temporary heat stupor, still higher a zone of more prolonged inactivity or dormancy (æstivation) limited above by the zone of fatal temperatures ; in the opposite direction we find the zones of cold stupor, of dormancy (hibernation) and of fatal low temperatures (Hunter and Pierce, 1912). All these zones and their limits naturally differ in cases of different insect species,

2887. Wt. P. 1071—2307. 375. 8/29. Wy. & S. Ltd. Gp. 2.

even of different sexes and stages of development of the same species; moreover, each kind of activity—movements, feeding, pairing, egg-laying, etc., has its more or less definite optimum zone. The differences in the temperature range of activities between different species of insects may be very striking; thus, certain grasshoppers are fully active at midday in the deserts of Palestine when the surface temperature reaches over 140°F. (Buxton, 1924), while some aphids have been observed active and copulating at 19°F. (Bachmetjev).

More detailed quantitative studies on temperature relations of insects have further shown that even the same individual may react towards a definite temperature in a different manner according to other external factors or internal conditions. Thus, woodboring larvæ of beetles freeze hard at –12·8°C, but only if the larva has been taken from its natural habitat in winter, while the same larva collected in summer freeze at –0·77°C. (Payne, 1927). This varying degree of cold hardiness in insects has been recently associated with the state of water in the insect body; namely, it has been found to depend on the balance between the free water which freezes easily and the water bound by colloids and hardly affected by low temperatures. This balance of water in its turn is connected with the moisture of the insect food, and with the general humidity of the habitat (Robinson, 1928). This one example already serves to demonstrate that the problem of the influence of temperature on insects has two different aspects, the meteorological and the physiological, the latter touching upon the still very obscure phenomena of the biochemistry and biophysics of colloidal substances.

The physiological side of the problem makes it imperative that the influence of the temperature on the insect should be studied in such a way that not only the external temperature conditions and the corresponding reaction of the insect are taken into account, but due attention is also paid to the ability of the insect to absorb and to utilize the heat of the surrounding medium. This was realised long ago and a series of studies dealing with the effects of external temperatures on the internal body temperatures of insects are now available. These studies have demonstrated first of all, that insects, although always considered to be cold-blooded animals, possess some power to adjust the internal body temperature by movements, and are, thus, not absolutely dependent on the external conditions (Bachmetjev, Pirsch). Much more important is the observation that the degree of absorption of radiant energy varies very widely in different insects, apparently mainly in connection with their coloration. The coloration of insects, particularly of butterflies, has received a great deal of attention from experimental entomologists, but it is only lately that views have been expressed as to the possible importance of coloration in the thermal economy of insects. Direct experiments on the influence of particular colours on the absorption of radiant energy are still practically lacking (Buxton,

1924), but there is no doubt that this is one of the most promising fields of research, in which an entomologist should work together with a meteorologist and a physiologist, so as not to overlook any of the factors influencing both the radiation and the absorption and transformation of radiant energy within the insect body.

Most of the above considerations refer not only to the visible activities of insects, but also to the internal processes of their development, in which temperature plays an extremely important part. Experimental work under controlled conditions of temperature permitted the formulation of the connection between the external temperatures and the rate of development of insects, in mathematical terms, but it must be admitted that we are still far from exact knowledge and understanding of the phenomena involved (Bodenheimer, 1926). The first idea of this connection was very simple; it was assumed that the development of an insect begins and stops at a definite temperature which was called the zero of development. It was further assumed that every degree of temperature above the zero acting during a day corresponds to a definite and equal advance in the development of an insect. With these assumptions it was easy to calculate the number of "day-degrees" necessary for the accomplishment of a certain stage of development, once the sum of effective temperatures for this stage had been determined experimentally. However, later investigations demonstrated that the conception of a constant sum of effective temperatures necessary to complete a stage is a fallacy and that the actual sum varies within very broad limits, making the practical use of the principle out of the question. For example the beetle *Sitodrepa panicea* requires 1,820 day-degrees at 20°C. and 3,638 at 17°C. The reason for this lies in the fact that the action of one degree of temperature during a definite period of time is not the same at different temperatures; in other words the value of day-degrees is not constant but may be 2–3 times as high at certain temperatures as at others. Special curves and formulæ have been constructed to express the relationship between temperatures and development and some of them (e.g., Blunck's formula) proved to be fairly useful for practical calculations of the period of time necessary for the accomplishment of a definite stage of development under certain conditions. It would carry us too far to discuss here all the details of this relationship, and I restrict myself to a broad indication of its main features. First of all, it must be realised that under the term development many very different internal processes are included, mainly the growth, the formation of genital products in the insect body and the formation and growth of the embryo in the eggs. As may be expected, all these processes are accelerated at a higher temperature, within the optimum limits, of course. As a result of this acceleration, each stage, and the whole life cycle of a given insect may be substantially different in length, according to the temperature, and this is reflected in the fact that certain insects develop only one complete generation a year

in colder climates and several annual generations in warmer ones ; the practical importance of this difference is obvious, since in the latter case there will be several periods of injurious activities, if the insect in question feeds on cultivated plants. The formulæ referred to above permit of the calculation of the number of annual generations of a given insect possible in any given locality, if the temperature conditions of the latter are known, and this is being done with a certain degree of exactitude (Bodenheimer, 1926). There are several reasons why absolutely exact results cannot be attained.

To begin with, the mean temperatures for more or less long periods, not shorter than a day, are usually made the basis of calculations, but such means do not correspond to the exact quantity of heat energy received by the insect during the period. Indeed, the latest work on these lines with the codling moth led the investigator (Shelford, 1927), to the conclusion that temperatures cannot be summed up correctly for biological purposes, unless readings are taken in intervals of one or two hours, throughout the whole period of the development of the stage in question. It is obvious that this method is extremely cumbersome. A still further source of inexactitude of the theoretical conclusions as compared with the actual course of events in nature depends on the fact that all our formulæ and curves are based on experiments at constant temperatures, while there is no constancy of temperature in nature, and mean temperatures for a given period have to be used in the calculations. Recent experiments have proved that the fluctuations in temperature exert a considerable accelerating influence on the rate of development of insects (Cook, 1927). Thus, daily fluctuations in the temperature are not without their direct importance. Similarly, the annual range of temperatures in temperate climates has its significance, quite apart from the arrest of development during the cold months ; it has been found for instance, that winter cold has an accelerating action on the rate of development of grasshopper eggs, which hibernate in soil and hatch in spring. The eggs kept throughout the winter at a constant temperature of 23°C. developed in 45 days, while the eggs kept in the open air for 39 days and then subjected to a constant temperature of 23°C. required only 40 days for their development (Bodine, 1925). The reasons for this somewhat surprising stimulating effect of fluctuations in temperature, and in particular of low temperatures, are still obscure, but this is a problem for a physiologist to solve and we may leave it alone.

An excellent illustration of the complexity of temperature relations of insects is presented by the differential effect of the same external temperature on an insect and its parasite. The rate of development of the wheat aphid *Toxoptera graminum* is faster than that of its parasite *Lysiphlebus tritici* ; the threshold of development for the host is 32°F., while for the parasite it is 36°. At a mean temperature of 68° a parasite would develop in 264 hours, and a host in 240 hours ; while the parasite was developing, a host female would have produced

26·4 young aphids. The parasite would ordinarily sting 22 aphids during the two days following its emergence, when the total progeny of one host female would be 31·2 individuals, thus being 9 individuals ahead of the parasite, which therefore, can never exterminate the host. It is easy to see how relatively small differences in the activity range of the host and the parasite and their rate of development as affected by temperature, may become a deciding factor in the abundance of both insects (Headlee, 1917 ; Shelford, 1926).

A somewhat parallel case is that of insects and certain micro-organisms associated with them, which are of exceptional interest, being the causative agents of the most dangerous human diseases. For example, temperature exerts a direct effect on the malaria parasite within the mosquito ; low temperatures, not in themselves injurious to the mosquito, inhibit the development of the parasite ; on the basis of this, it is possible to define the areas and seasons which are dangerous from the point of view of malarial infection through mosquitos (Gill, 1921). With regard to the plague bacilli which are carried by fleas it has been found that a temperature of 85°F. (29·44°C.) caused a more rapid disappearance of the bacilli from the stomach of fleas than that of 70°F., while at the low mean temperature of 50°F. infected rats often died before plague bacilli appeared in their blood, so that their fleas had no chance to become infected (Rogers, 1928). Further highly interesting observations refer to the effect of temperature on certain symbiotic micro-organisms of locusts, in which they live at normal mean temperatures without any apparent harm to the host, but at low temperatures the symbionts tend to increase to such an extent that the development of genital products of the locust is inhibited and a fatal disease may follow. In other cases, normally saprophytic fungi proved capable of becoming dangerous parasites of caterpillars at sufficiently high, though not in themselves injurious temperatures.

The effects of the temperature factor on the geographical, topographical and seasonal distribution of insects will be discussed later, as humidity has also to be taken into consideration, and we must first review the available information on the influence of this factor by itself.

Humidity and Precipitation.—Although exact quantitative observations on the effects of the relative humidity of air on insect activities are not yet sufficiently numerous, the data accumulated enable one to conclude that the scheme of the relations of insects to humidity is essentially the same as that with regard to temperature. In other words, it may be assumed that a zone of optimum humidity, as well as upper and lower fatal limits exist for each species and each stage of its development. There is no doubt, however, that variations in this respect are still greater than in the case of temperature, since the physiological influence of the humidity of air on the insect must be less direct than that of its temperature. Indeed, insects

obtain most of the water necessary for their internal physiological processes with their food and not from the air, so that the main influence of the water vapour contained in the air is through evaporation, which we will discuss later. There are direct indications that the water obtained with food may make an insect practically independent of the atmospheric humidity ; thus, the aphid *Toxoptera graminum* feeding on sap of grasses takes six days from birth to maturity under a constant temperature of 80°F. and relative humidities ranging from 37 per cent. to 100 per cent. (Headlee, 1914). Moreover, even eggs of some insects (e.g., cotton seed bug *Oxycarenus hyalinipennis*) (Kirkpatrick, 1923), do not show any difference either in the percentage of hatching or in the length of development in relative humidities ranging from one to 100 per cent. ; in this case, however, a possibility that the evaporation was prevented by the shells of the eggs is not excluded. Other experimental data on the subject show somewhat varying results and a definite rule as to the influence of relative humidity of the air on the rate of development of insects cannot, at least at present, be laid down. This conclusion may be explained by the fact that the concentration of body fluids differs widely in different insects and in the same insect during its development, so that similar conditions of atmospheric humidity may have very different physiological effects, the same relative humidity being fatal in one case, and representing optimum conditions, or being without any importance, in another.

One important effect of high humidity of air is that at certain temperatures it is highly favourable to the development of various fungous diseases of insects and thus becomes an indirect controlling factor.

Data with regard to the influence of *precipitation* on insects, cannot of course be very exact, since the effects of the precipitation are bound to be mainly indirect, acting through the corresponding changes in the evaporation and therefore, being closely connected with temperature, wind, atmospheric pressure, etc. Another effect of precipitation is the change in the moisture content of the soil which is highly important, since a great percentage of insects pass one stage or another in the soil. These problems involving more than one factor will be discussed later.

The direct effects of rain on insects are mainly mechanical and consist in the destruction of more tender stages, or in the drowning, particularly by rainstorms ; there are cases on record which show the great controlling value of this factor. A very common example of the direct influence of rainfall is its effect on the emergence of insects from quiescent stages, *i.e.*, from eggs or pupæ, or from hibernation. The effects are partly due to the mechanical action of water on the outer coverings of pupæ (cocoons) or egg-shells, which can be burst only when softened, while in some cases the effects must be connected with the absorption of water necessary for completing the development of the stage or the resumption of the physiological activities.

Indirect controlling influence of rainfall through the vegetation is very important. Apart from those cases when drought conditions cause a mass destruction of phytophagous insects through lack of their food-plants, the connection between rainfall and the abundance of an insect is often very obvious and undoubtedly indirect, *i.e.*, through the vegetation. Outbreaks of certain bark-beetles for example, are definitely connected with the periods of rainfall deficiency. On the other hand the propagation of certain insects, like aphids, is favoured by increased rainfall, provided the rains are not sufficiently heavy to cause their mechanical destruction.

Perhaps most important of all is the distribution of rainfall throughout the year. Usually this factor acts in conjunction with the seasonal temperature regime, but there are cases of the influence of rain alone. Thus the most important factor in the balance of the coffee-borer (*Stephanoderes hampei*, Ferr.) in Java and Sumatra is the distribution of rainfall throughout the year. In certain areas it rains at all seasons and the flowering of coffee-plants and ripening of berries is spread over the whole year, so that the insects find food continually and their generations follow each other without interruption. In other districts the east monsoon brings with it a dry period of several months duration, and the west monsoon is accompanied by continuous rains, which prevent the flowering of coffee. Thus a period when no food is available for the pest is interpolated each year and during this period the beetles die out, with the exception of few survivals (Friedrichs, 1925). Another example of indirect influence of rainfall is presented by the tsetse fly (*Glossina morsitans*) which is closely connected with shady forests ; the leaf fall in African forests is dependent mainly on the rains and thus the latter become an important factor in the seasonal movements of the fly (Swynnerton, 1921).

Very little data exist with regard to other forms of precipitation besides rain. Snow has an important function as a protection from winter frosts of insects hibernating in the soil or on its surface. Hail has been recorded to cause great mechanical destruction of various insects, but the controlling value of this factor is, of course, practically negligible.

Wind.—There can be no direct influence of any movements of air on the development of insects, but the activities, particularly of those insects which use their wings for flight, are bound to be affected by winds. In most cases the influence is negative, at least as regards winds of higher velocities, but it must be confessed that quantitative observations in this direction are practically lacking. The relations of flying insects to wind are still insufficiently studied, though certain observations on the flight of nocturnal insects tend to show that many of them are inclined to fly against the wind and not with it. However, no general rule can be laid down (Lutz, 1927). A number of exact observations have been made on the wind dispersal

of insects, demonstrating clearly the importance of winds in this respect. It was found that normal dispersion of a number of insects, like the Hessian fly, Gipsy moth, etc., depends on prevailing winds perhaps more than on any other agency (Webster, 1902; Collins, 1915). There are some cases on record which illustrate the importance of winds in carrying insects over unexpectedly long distances, as for example the appearance of winged spruce aphids on the snow at Spitzbergen, where they could have been brought only by wind from the Kola Peninsula—a distance of over 800 miles in a straight line (Elton, 1925). Tropical cyclones must be particularly powerful agents in the dispersion of insects from island to island, but so far the actual data are neither numerous nor sufficiently exact.

The importance of the upper air currents in the dispersal of insects has been stressed recently (Felt, 1928), but the evidence in favour of this view is very meagre and exact observations of the insect fauna of the upper layers of atmosphere are badly needed.

Indirect action of winds as a factor of evaporation must also be of great importance.

Atmospheric Pressure.—Direct effects of atmospheric pressure on insects are substantially different from those on higher animals, probably owing to the fundamental difference in the respiratory and circulatory organs. Experiments on the influence of a vacuum on insects gave very surprising results, since bumble-bees subjected to a super-vacuum of $\frac{1}{1000}$ mm. for 90 seconds and then suddenly returned to the normal pressure remained unharmed and active (Lutz, 1929). This shows that ordinary changes in pressure occurring in nature can be hardly of any direct importance in insect life, at least, not as controlling factors.

At the same time, there is some evidence that the general activities of many insects increase with barometric depressions, and there are also definite and sufficiently exact observations and experiments on the influence of depressions on the length of the pupal period of butterflies and moths, as well as on their emergence from the pupæ. It has been found that a uniform normal pressure maintained throughout the pupal period prolongs the latter, while a uniform reduced pressure shortens it considerably (e.g., in *Pieris rapae* the stage lasted only 9 days at pressure 710–728 mm. instead of the normal 15 days). The emergence of adults in the great majority of cases does not take place except on the fall of barometric pressure, a diminution of pressure by one millimeter being sufficient to induce the eclosion of an adult which is ready for it. The action of pressure on eclosion must be purely mechanical: the adult insect within the pupal skin is unable to burst it until a drop in atmospheric pressure creates a difference between the latter and the pressure of the body fluids (Pictet, 1917).

It must be admitted that observations on the direct influence of pressure on insect activities and development are still very fragmentary.

Indirect influence of pressure is through winds and evaporation and does not need a separate discussion.

Atmospheric Electricity.—No exact data exist in this respect, but it is generally known that many insects, especially the nocturnal ones, are more active before a thunderstorm.

Light.—Observations have been made which tend to show that the production of sexual forms in aphids depends on the direct action of light, since under experimental conditions sexual forms were produced earlier and more abundantly in the case of shorter exposures to artificial light, while long exposure had an inhibiting influence (Marcovitch, 1924). These observations were contradicted by other observers and final conclusions must be deferred. Further studies of light as a factor of development are highly desirable, since light has been greatly neglected in the past.

The influence of light on activities of insects has not been sufficiently studied, though the existence of strictly diurnal and nocturnal insects already shows that the reactions of different species towards light are very dissimilar. So far, however, exact observations on the quantity and quality of light necessary for various activities are very scarce and of uncertain value.

Combination of Factors.—The most important complex factor exerting very great influence both on the activities and on the development of insects is the evaporating power of air, which depends on the temperature, humidity, air movements and atmospheric pressure. Physiological reasons for the importance of this factor are obvious, since all biological processes take place in a liquid or semi-liquid medium, and the deficiency or the excess of water in the organism is bound to affect the rate, or even the direction of the process. Indeed, it is almost certain that evaporation causes an insect to react very differently towards the same temperature if the relative humidity varies. For example, the cotton seed bug dies after 150 hours' exposure to 25°C. at 60 per cent. humidity, but at 80 per cent. humidity the exposure must be twice as long to be fatal (Kirkpatrick, 1923) ; it is very probable that death from high temperature is due to excessive loss of water, which is greater at lower humidities. On the other hand, very high humidities may be injurious through preventing evaporation, which tends to lower the body temperature and thus to moderate the influence of heat. Another case of combined effect of humidity and temperature is presented by the resistance of insects to very low temperatures. This resistance depends greatly on the water content of the insect ; low evaporation rate makes hibernating insects less resistant to freezing through increasing their water content (Payne, 1927). As regards the development of insects, several investigators found that its rate is increased at lower humidities, though the temperature conditions remain the same. This must also be connected with the rate of evaporation.

In view of these and similar facts, it is only natural that many entomologists consider observations on the evaporating power of air highly important for their purposes. They are probably right, at least in considering that these observations present the simplest method of evaluation of the combined effect of practically all the main meteorological factors. However, it must not be forgotten that this method makes the appreciation of the exact value of each separate factor more difficult ; the exact quantitative analysis of factors should be the aim of ecological investigations.

Very little data exist with regard to combined action of other meteorological factors, except those involved in evaporation. Light in combination with temperature and perhaps with humidity may be a controlling factor in certain activities of insects. For example, the codling moth lays its eggs only in the dark, and only at a temperature not below 62°F.; if the temperature falls below that figure before it is sufficiently dark, no eggs are laid. Thus the propagation of the species depends on the favourable combination of the two factors—absence of light and temperature (Iselby and Ackerman, 1923). Diurnal insects, on the other hand, are more sensitive to light at higher temperatures and an optimum combination of the two factors may be of the greatest importance for the species.

Climate and Weather.—With this preliminary acquaintance with the influence of various meteorological factors on insects, we can now turn our attention to the main general effects on them of climate and weather. These effects may be conveniently grouped under two headings—distribution of insects in space (geographical and ecological) and their distribution in time (seasonal and periodic cycles).

Geographical and Ecological Distribution.—It is not proposed to discuss here the various means of dispersal of insects ; it is sufficient to say that each species has a natural tendency to spread as widely as possible and every possible agency is utilised for this purpose, so that there is a theoretical possibility for each species to populate the whole surface of the earth. This possibility is, however, very seldom realised, and the number of truly cosmopolitan insects is very small ; practically all of them, moreover, live in close association with man, *i.e.*, under conditions which make them independent of the differences in the natural conditions of various countries. The great majority of the remaining insects are restricted to more or less definite geographical areas, and the factors limiting their distribution are almost entirely climatic since the geological factors of distribution also depend mainly on changes of climates throughout the ages.

The area of distribution of an insect species is obviously that in which the combination of all climatic and biotic factors permits its survival. It is usually considered that every organism is adapted perfectly to the conditions of its existence, but this seems to be a

principle based on theoretical considerations and not in accordance with facts. Indeed, recent studies on the climatic factors controlling insects appear to emphasize that the percentage of survival of progeny is normally very small, the bulk succumbing to the numberless adverse influences of the normal environment. In other words, insect species survive not because of their wonderful adaptation to environment, but in spite of their insufficient adaptation and owing to their high reproductive abilities. Indeed, these abilities are such, that given really optimum conditions of existence, almost any insect species would become exceedingly abundant within a short time, as is proved by periodic mass outbreaks of injurious insects, dependent mainly on the optimum combination of all factors.

The climatic factors limiting the area of distribution of an insect are mainly temperature and humidity, or the evaporating power of air dependent primarily on them. Thus, the northern limit of the brown tail moth in North America coincides with the minimum isotherm-35°C., while the asparagus beetle (*Crioceris asparagi*) cannot extend its range beyond the minimum isotherm-10°C. (Sanderson, 1908). The cabbage butterfly (*Pieris brassicae*) reaches its southern limit of distribution in Palestine, since it can successfully live there only in winter months, while the summer heat kills nearly 100 per cent. of eggs and young larvæ (Bodenheimer, 1928).

Humidity in itself is undoubtedly a very important factor of distribution, but the data on its limiting rôle are few and inexact. Much better studied is the combined effect of temperature and humidity, or temperature and precipitation, and in this direction great advances have been made recently, owing to the extensive use of Ball-Taylor climographs and hythergraphs, which permit the correlation of the distribution of an insect with the two main climatic factors (Cook, 1924; Shelford, 1926; Tehon, 1928). Their application demonstrated, in particular, that it is often not the absolute averages of temperature and humidity, or their maxima and minima that limit the distribution, but the seasonal temperature and rainfall régime. This is easy to understand since an insect has its own seasonal cycle and its different stages of development have different requirements.

The practical use of climographs in entomology is especially important in the case of insect pests introduced, as happens very often, from one country to another. Climographs of the original home of the insect permit us to understand the conditions of its existence there, and a study of climographs of the new country enables us to judge what are the chances of its acclimatisation in particular areas there.

The method of climographs has, however, its limitations. One reason for its inexactitude lies in the fact that it is based on mean monthly temperatures and humidities, while we know the great importance of fluctuations in both for insects. Another and much greater source of error lies in the fact that climographs have to be

based on the data provided by meteorological stations. Meteorologists, for obvious and excellent reasons of their own, adopted certain standardised methods of taking observations, and this standardisation makes many of their data of very little value to us. Temperature readings taken in Stevenson screens and then reduced to the sea-level value, have obviously a very distant relation to the temperatures to which insects are normally exposed, while the hours of taking observations are fixed, naturally, without any regard to various activities of insects. The same remarks apply to observations on relative humidity. The fact is that the climate of a locality as studied by meteorologists has probably much less significance for insects than the micro-climates of the widely varying habitats of insects. Detailed observations on temperature and humidity in a forest, for instance, show that the means and the range of daily, monthly and annual fluctuations differ widely at different heights from the ground (Weese, 1924). This means that standardised observations taken near, or even in the forest, would not express the conditions of existence of most of the forest insects.

Similarly, the exposure of slope, the relative density of vegetation, slight depressions of surface, etc., all affect the micro-climate and make standard observations inapplicable in each particular case. The problem becomes even more complicated in the case of insects living inside plants, or parasitic on other animals, or otherwise isolated from the direct influence of meteorological factors, though still dependent on them indirectly. It has been found, for example, that the temperature within an open boll of the cotton plant (in which several important pests live) is lower than the shade temperature during the day, while at night the minimum within the boll is above that of the air (Kirkpatrick, 1923). In the case of desert insects, it has been found that a great number of them pass the day burrowed into soil, or in caves, etc., coming out only at night, with the result that their conditions of existence have a very remote relation to the desert climate as represented by ordinary meteorological data (Williams).

All these considerations show that exact knowledge of meteorological factors limiting the distribution of an insect can be only obtained through detailed and prolonged studies of the micro-climate of its habitat, or rather habitats, since most insects change their habitat during development, the larvæ, e.g., feeding openly on foliage, the pupa being buried in the soil, the adult flying about, and the eggs being concealed under the bark of a tree, etc. The problem, thus, becomes bewildering in its complexity, and its successful study depends only on the realisation of difficulties and their solution by the combined efforts of entomologists and meteorologists.

While stressing the importance of micro-climatic observations, I am far from implying that the standard meteorological data are quite useless for entomological purposes. On the contrary, as I have already said, some very valuable practical results have been

obtained by studies of climographs in connection with the distribution of insects. This is only natural, since in these studies climographs serve for comparison of two or more climates, and the relation of climatic factors as observed under standard conditions to the micro-climates of definite habitats in different countries must be essentially the same. I would even venture to suggest that it might be possible after careful studies to find out the relation for each particular case, e.g., to find an empirical formula, which would permit the calculation of the temperature within a cotton boll from the standard readings of temperature.

On the other hand, the importance of meteorological data for various local agricultural and biological problems is so very great that it would be legitimate on the part of representatives of those sciences to ask meteorologists to consider some alterations, or amplifications of the standard methods of taking observations in order to make them more readily utilised.

Cycles and Periodicity.—Seasonal periodicity in insect life is commonly known, and its direct dependence on annual fluctuations of temperature in colder regions appears obvious. Recent studies, however, throw some doubt on the popular idea that it is only the winter cold which is directly responsible for the phenomenon of hibernation, i.e., the state of more or less complete inactivity, in which most insects pass the winter. Indeed, it was found that in cases of insects normally hibernating, e.g., in the egg stage, the eggs cannot be brought to development, even if kept at sufficiently high temperature. Facts of this kind point to the existence in insects of our latitudes of an inherited, fixed annual cycle of development, which is not easily altered by external conditions. There is little doubt, however, that this fixed cycle is due not to some mysterious agency, but has developed in the course of thousands of generations as a direct response to the environment.

Hibernation of insects presents special interest for our problem, since in this state of inactivity they are more than ever subject to unfavourable meteorological influences, and the winter mortality of hibernating stages is usually very high. It is worth mentioning that this mortality is much less due to the direct action of cold than may be supposed. Indeed, all known facts support the idea that long, severe winters, with frost and snow, do less harm to hibernating insects than milder winters with intermittent frosts and rains. This is due to the fact that most insects can survive even repeated freezing without any harm, provided their water balance is properly adjusted, while mild moist winters tend to disturb the balance unfavourably with disastrous results; besides, various fungous and bacterial diseases of insects develop more readily in mild weather.

The great majority of insects of temperate climates have only one complete generation a year; some take several years to develop, while there are many which have a shorter period of development

and are able to produce several generations in one year. In the case of the last-named group, the number of generations per annum naturally differs according to the latitude, and this affects the relative economic importance of an injurious insect in different countries. Since the rate of development depends, as we know, mainly on the temperature, it is possible, by means of certain formulæ mentioned above, to calculate the possible number of annual generations of a pest in any given country. Some more or less successful attempts in this direction have been made.

While we have some knowledge of the annual cycle of insects in temperate climates and of its causes, the same cannot be said with regard to sub-tropical and tropical areas. Theoretically, it would appear that the development of insects there should go on without interruption all the year round, and as many generations be produced as are consistent with the length of the period required for one full generation. This is, however, not so, and many tropical insects seem to have definitely only one annual generation. However, I must stress that exceedingly little is known on this subject. The interesting fact about insects of hot climates is that many of them have their resting stage also, corresponding to the hibernating stage of insects of higher latitudes, but not connected with temperature. The factor regulating the annual cycle of insects in hot climates appears to be the humidity of air and of the soil, and the resting stage normally corresponds to the dry period. It has to be admitted, however, that the phenomenon of aestivation, as it is called, is still very little studied. Hibernation and aestivation present major correlations of the annual life cycle of insects with the seasonal weather, and side by side with them there is a number of minor adjustments which are none the less important for the insects themselves, and for man. There are various phenomena of phenological order, i.e., the appearance of different stages in development and their transformation, which should be studied in connection not only with the weather conditions, but also with the corresponding seasonal phenomena in the plant world. The importance of exact correlation of the appearance and development of an insect and of its food plant is often very great. Thus, the apple-blossom weevil (*Anthonomus pomorum*) lays its eggs in flower-buds of apple, and the larva must not only hatch, but fasten the unopened petals from the inside by a web, before the flowers begin to open; if the spring is cool and the buds mature and open slowly, the progeny of the weevil is safe, but in hot weather it happens often that the flowers open before the newly-hatched larvæ have time to prevent them from doing so and the larvæ fall out and die. In this way the life of insects and the degree of their economic importance depend on very small fluctuations of meteorological factors, which may affect the plant and the insect in a slightly different way, and thus turn the balance between them in favour of one and to the detriment of the other.

Extensive studies in the phenology of insects and plants led the American entomologist Hopkins to formulate his bioclimatic law, the main point of which is that "other conditions being equal, the variation in the time of occurrence of a given periodical event in life activity in temperate North America is at the general rate of 4 days to each one degree of latitude, 5 degrees of longitude, and 400 feet of altitude, later northward, eastward and upward in spring and early summer, and the reverse in late summer and autumn." This law is purely empirical, and its theoretical significance is limited, while the practical application is possible only in normal seasons and under equable ecological conditions, which two requirements are seldom satisfied. Further, the law holds fairly good for North America only and attempts made by its author to extend it to other continents remained theoretical, without a practical test, at least as regards insect phenology.

Much more promising are the attempts to base the forecasting of seasonal phenomena in the life of insects on the series of controlled experiments which supply the necessary data on the standard average period for the completion of a certain stage of development under controlled conditions of temperature and humidity. If meteorological observations are then carried out throughout the period of development of the stage in nature, and the results are summed up, it becomes possible to predict the completion of the stage and the appearance of the next one some time before it happens in nature. Such a forecast may be of great practical importance, for example in the case of the codling moth, where it is necessary to spray as near as possible to the time of hatching of the larvæ from the eggs (Shelford, 1927). The practical application of this method is, however, greatly limited, since it requires, first, a very extensive series of experiments under controlled conditions, with the use of complicated and expensive apparatus, and secondly, the taking of readings of temperature and humidity at 1–2 hourly intervals throughout a considerable period.

Apart from the seasonal rhythm in the appearance and activities of insects, there is a more or less strongly marked periodic fluctuation of a species from year to year. Only relatively few insect pests are equally numerous and injurious every year, while most of them are practically negligible, except in certain years, when mass outbreaks occur. It would be out of place to discuss here all the causes for these periodic fluctuations, but I would like to point out that recent researches in this direction tend to throw some doubt on the commonly accepted idea that the chief controlling factor is the parasites, since a number of cases have become known in which the factors normally keeping an insect species down are almost entirely of meteorological order. This has been admitted for the cotton boll weevil in America (Hunter and Pierce, 1912), for the corn-borer in Europe (Thompson and Parker, 1928), for the almond sawfly in Palestine (Bodenheimer, 1928), for the cotton seed bug in Egypt (Kirkpatrick, 1923), for plague

fleas in India (Hirst, Rogers), for vine-moths in Europe (Stellwaag, 1925), and for some other notorious pests. The underlying principle of the fluctuations in number of insects resulting from climatic factors is that the optimum range of each factor is often relatively narrow, and a realisation of optimum conditions for the complete set of factors leading to an outbreak can occur only at irregular intervals, sometimes only after a series of favourable years. Dependence of the fluctuations on meteorological factors has often been suggested on the basis of the general impression that a certain pest becomes abundant, e.g., in very dry years, but it is only recently that the study of the relations of insect outbreaks to climatic factors obtained a firmer footing through the use of climographs. It is now more and more customary, when studying an injurious insect, to construct climographs for a series of years, or for several localities, and, by comparing and correlating them with the relative abundance of the insect, to obtain an idea as to the climatic conditions favourable to its outbreaks. Since three quantities, viz., temperature, humidity and the abundance of pest, enter into the scheme, it has lately been suggested that three-dimensional graphs should be used to express their inter-relations. Such graphs have not yet been subjected to sufficient tests, and their practical utility cannot be considered as proved, although theoretically they present the only correct solution of the problem.

What has already been said with regard to the shortcomings of climographs in the studies of distribution of insects, holds good in the application of climographs in the studies of the fluctuations in the abundance of an insect. It must be realised that only approximate conclusions can be made with regard to the value of one, or the other, of the climatic factors involved in the periodic fluctuations, as long as the climographs are based on the standard meteorological data, and not on the micro-climatic observations in the actual habitat of the insect under investigation. Another way out is a study of the correlation between standard meteorological data and the micro-climatic conditions of the habitat, so that the standard data can be converted to represent the micro-climate, but this has not yet been attempted.

If the relative abundance of an insect and its fluctuations have been studied on the basis of a large number of data, the deductions obtained may be used for forecasting the possibility of an outbreak of the insect. For example, outbreaks of the American pale western cutworm (*Porosagrotis orthogonia* Morr.) have been found to depend on the total amount of rainfall in May, June and July of the preceding year ; the critical amount of precipitation varies with the temperature and produces a definite critical soil moisture. If the moisture exceeds the critical amount, the number of cutworms decreases in the following year ; if the moisture be less than the critical amount, the number of cutworms increases. The effect is cumulative and severe outbreaks may follow a series of dry years (Cook, 1927).

In this case the possibility of forecasting an outbreak is clear, and there is little doubt that the climograph method will prove its usefulness in this respect in many other cases, if properly applied and based on sufficient data. At the same time, it must never be forgotten that the factors controlling the abundance of an insect may be, and often are, other than temperature and humidity, so that a blind application of climographs to every case would be unreasonable.

My present survey of the problem of the relations of insects to weather and climate has been much too brief to permit the discussion of all its aspects. I hope, however, that I have at least succeeded in one of my aims—namely to illustrate the importance to entomologists of meteorological and climatological studies. There is a vast number of entomological problems which cannot be solved without the friendly help of meteorologists, and it is to be hoped that a close co-operation between these two sciences will rapidly develop in the immediate future.

Bibliography.—A survey of the literature on the subject of relation of meteorological factors to insects is being prepared, and a complete bibliography will be published later. The following list includes the titles of some of the more important papers referred to in the present brief summary.

Bachmetjev, P. 1901. Experimentelle entomologische Studien vom physikalisch-chemischen Standpunkt aus. 1. 160 pp., 7 fig.

Bachmetjev, P. 1907. Experimentelle entomologische Studien vom physikalisch-chemischen Standpunkt aus. 2. 944 pp., 31 figs.

Blunck, H. 1923. Die Entwicklung des *Dytiscus marginalis* L. vom Ei bis Imago. 2. Die Metamorphose.—*Ztschr. wiss. Zool.* 121. 171–391, 44 figs.

Bodenheimer, F. S. 1926. Uber die Voraussage der Generationenzahl von Insekten. III. Die Bedeutung des Klimas für die landwirtschaftliche Entomologie.—*Ztschr. angew. Ent.* 12. 91–122, 6 figs.

Bodenheimer, F. S. 1928. Welche Faktoren regulieren die Individuen-Zahl einer Insektenart in der Natur.—*Biol. Zentralbl.* 48. 714–739, 4 figs.

Bodine, J. H. 1925. Effect of temperature on rate of embryonic development of certain Orthoptera. *Jour. Exper. Zool.*, 42. 91–109.

Buxton, P. A. 1924. Heat, moisture and animal life in deserts.—*Proc. Roy. Soc., London*, B. 96. 123–131, 3 figs.

Collins, C. W. 1915. Dispersion of gipsy-moth larvæ by the wind.—*U.S. Dept. Agr. Bull.*, 273. 23 pp., 6 pls., 8 tables, 1 map.

Cook, W. C. 1924. The distribution of the Pale Western cutworm, *Porosagrotis orthogonia* Morr.; a study in physical ecology.—*Ecology*, 5. 60–69, 7 figs.

Cook, W. C. 1927. Some effects of alternating temperatures on the metabolism of cutworm larvæ.—*Jour. Econ. Ent.* 20. 769–782, 7 figs., 4 tables.

Elton, C. S. 1925. The dispersal of insects to Spitzbergen.—*Trans. Ent. Soc. London.* 289.

Felt, E. P. 1928. Dispersal of insects by air-currents.—*N. York State Mus. Bull.* 274. 59–129.

Friedrichs, K. 1925. Der Kaffeebeerenkäfer in Nederlandisch-Indien.—*Ztschr. angew. Ent.* 11. 325–385, 18 figs.

Gill, C. A. 1921. The influence of humidity on the life history of mosquitos and on their power to transmit infection.—*Trans. R. Soc. Trop. Med. & Hyg.* 14. 77–83.

HEADLEE, T. J. 1914. Some data on the effect of temperature and moisture on the rate of insect metabolism.—*Jour. Econ. Ent.* 7. 413–417.

HIRST, L. F. 1926–27. Researches on the parasitology of plague.—*Ceylon Jour. Sci.* Sect. D, 1. 155–455, pls., maps.

HOPKINS, A. D. 1918. Periodical events and natural law as guides to agricultural research and practice.—*Mon. Weather Review.* Suppl. No. 9. 42 pp., 24 figs.

HUNTER, W. D., and PIERCE, W. D. 1912. Mexican cotton-boll weevil. —*U.S. Dept. Agr. Bull.* 114. 118 pp., 22 pls., 34 figs.

ISELY, D., and ACKERMAN, A. J. 1923. The life history of the codling-moth in Arkansas, with special reference to factors limiting abundance. —*Arkansas Agr. Exp. Sta. Bull.* 189. 57 pp., 3 pls., 3 figs.

KIRKPATRICK, T. W. 1923. The Egyptian cotton seed bug (*Oxycarenus hyalinipennis* Costa).—*Min. Agr. Egypt. Bull.* 35.

LUTZ, F. E. 1927. Wind and the direction of insect flight.—*Amer. Mus. Novit.* 291. 4 pp., 1 graph, 1 table.

LUTZ, F. E. 1929. Experiments with "wonder creatures."—*Natural History, N. York,* 29. 160–168, 2 figs.

MARCOVITCH, S. 1924. The migration of the Aphidae and the appearance of the sexual forms as affected by the relative length of daily light exposure.—*Jour. Agr. Res.* 26. 513–522.

PAYNE, N. 1927. Freezing and survival of insects at low temperatures.— *Jour. Morph.* 43. 521–546.

PICTET, A. 1917. Influence de la pression atmospherique sur le developpement des Lepidopteres.—*Arch. Sci. Phys. Hist. Nat. Geneve* (4) 44. 413–454, 1 pl., 4 figs.

ROBINSON, W. 1928. Relation of hydrophilic colloids to winter hardiness of insects.—*Collodium Symposium Monograph, N. York,* 5. 199–218, 9 figs.

ROGERS, L. 1928. The yearly variations in plague in India in relation to climate: forecasting epidemics.—*Proc. Roy. Soc. London,* B. 103. No. B721. 42–72, 4 charts, 1 map.

SANDERSON, E. D. 1908. The influence of minimum temperature in limiting the northern distribution of insects.—*Jour. Econ. Ent.* 1. 245–262.

SHELFORD, V. E. 1926. The relation of abundance of parasites to weather conditions.—*Jour. Econ. Ent.* 19. 283–289, 2 figs.

SHELFORD, V. E. 1927. An experimental investigation of the relations of the codling moth to weather and climate.—*Bull. Illinois Nat. Hist. Survey,* 16. 311–440, 34 figs., 28 tables.

STELLWAAG, F. 1925. Die Massenbewegung der Traubenwickler im Verhältnis zur Witterung.—*Anz. Schädlingskunde,* 1. 52–54, 63–64.

SWYNNERTON, C. F. M. 1921. An examination of the tsetse problem in North Mossurise, Portuguese East Africa.—*Bull. Ent. Res.* 11. 315–386, 9 pls., 1 map.

TEHON, L. R. 1928. Methods and principles for interpreting the phenology of crop pests.—*Bull. Illinois Nat. Hist. Survey.* 17. 321–346, 18 figs.

THOMPSON, W. R., and PARKER, H. L. 1928. The European corn borer and its controlling factors in Europe.—*U.S. Dept. Agr. Techn. Bull.* 59. 62 pp., 21 tables, 3 figs.

WEBSTER, F. M. 1902. Winds and storms as agents in the diffusion of insects.—*Amer. Natur.* 36. 795–801.

WEESE, A. O. 1924. Animal Ecology of an Illinois Elm-Maple forest.— *Illinois Biol. Mon.* 9. No. 4, 93 pp., 7 pls.

WILLIAMS, C. B. 1923. A short bio-climatic study in the Egyptian desert. —*Min. Agr. Egypt, Bull.* 29. 20 pp. 11 figs.

WILLIAMS, C. B. 1924. Bio-climatic observations in the Egyptian desert in March, 1923.—*Min. Agr. Egypt Bull.* 37. 18 pp., 10 figs.

WILLIAMS, C. B. 1924A. A third bio-climatic study in the Egyptian desert. —*Min. Agr. Egypt. Bull.* 50. 32 pp., 7 figs.

PUBLICATIONS ARISING OUT OF THE IMPERIAL AGRICULTURAL RESEARCH CONFERENCE, 1927.

Report and Summary of Proceedings. Price 1*s.*; with postage 1*s.* 5*d.* Obtainable from the sale offices of His Majesty's Stationery Office, or from the Office of the Ministry of Agriculture and Fisheries, 10, Whitehall Place, London, S.W.1.

Contains a full account of the events leading up to the Conference, the recommendations made, and the views expressed by the highest authorities in agriculture in all quarters of the Empire. 250 pages.

Abstract of Papers. (Two volumes.) Price 1*s.* net each. Post free. Obtainable from the Office of the Ministry of Agriculture and Fisheries, 10, Whitehall Place, London, S.W.1.

Containing abstracts of upwards of 500 papers on agricultural research in Great Britain and Northern Ireland during (1) the year October, 1926, to September, 1927; (2) the year October, 1927, to September, 1928.

List of Agricultural Research Workers in the Empire. Price 1*s.* net. Post free. Obtainable from the Office of the Ministry of Agriculture and Fisheries, 10, Whitehall Place, London, S.W.1.

Facilities for Advanced Study and Research in Agricultural Science and Cognate Pure Sciences in the United Kingdom. Price 1s. net. Post free. Obtainable from the Office of the Ministry of Agriculture and Fisheries, 10, Whitehall Place, London, S.W.1.

Opportunities for Students of Biology. Two leaflets containing notices to Parents and Students and Teaching Authorities. Free and post free. Obtainable from the Office of the Ministry of Agriculture and Fisheries, 10, Whitehall Place, London, S.W.1.